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THE CONTEMPORARY EVOLUTION OF MAN.

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In the past decade of practical research and speculation in biology two subjects have outstripped in interest and importance the rapid progress all along the line. These are, first, the life-history of the reproductive cell from its infancy in the ovum onward, and second, the associated problem of heredity, which passes insensibly from the field of direct observation into the region of pure speculation.

As regards the cell it was generally believed that the nucleus was an arcanum into the mysteries of which we could not far penetrate; but this belief has long been dispelled by the eager specialist, and it is no exaggeration to say that we now know more about the meaning of the nucleus than we did about the entire cell a few years ago. At that time the current solution of the heredity problem was a purely formal one; it came to the main barrier, namely, the relation of heredity and evolution to the reproductive cells, and leapt over it by the postulate of Pangenesis. The germ-cell studies of Balfour, Van Beneden, the Hertwig brothers, Weismann, Boveri and others have gradually led us to hope that we shall some day trace the con-

[1]Delivered before the Alumni of the College of Physicians and Surgeons, New York, February 12th, 19th, 26th.

nection between the intricate metamorphoses in these cells and the external phenomena of heredity, and more than this, to realize that the heredity theory of the future must rest upon a far more exact knowledge than we enjoy at present of the history of the reproductive cell both in itself and in the influence which the surrounding body cells have upon it.

These advances affect the problem of life and protoplasm, whether studied by the physician, the anthropologist or the zoologist, thus concentrating into one focus opinions which have been formed by the observation of widely different classes of facts. As each class of facts bears to the observer a different aspect and gives him a personal bias, the discussion is by no means ironical, and it is our privilege to live through one of those heated periods which mark the course of every revolution in the world of ideas. Such a crisis was brought about by the publication of the theory of Darwin, in 1858, and after subsiding has again been roused by Weismann's theory of heredity, published in 1883.

This is the situation I have ventured to present to you as Cartwright lecturer, not, of course, without introducing some conclusions of my own, which have been derived from vertebrate palæontology, but which I shall direct mainly upon human evolution.

So far as theories need come before us now, remember that Lamarck (1792) attributed evolution to the hereditary transmission to offspring of changes (acquired variations) caused by environment and habit in the parent. Darwin's latest view was that evolution is due to the Natural Selection of such congenital variations as favored survival, supplemented by the transmission of acquired variations. Weismann entirely denies the transmission of acquired variations or characters, and attributes evolution solely to the natural selection of the individuals which bear the most favorable variations of the germ or reproductive cells. We must, therefore, clearly distinguish between "congenital variations" which are part of our inheritance and "acquired variations" which are due to our life-habits; the question is, Are the latter transmitted?

Significance of Anomalies.—At the outset I would emphasize the extreme complexity of evolution by a few words upon Variation, or in terms of medical science, upon anomalies.

When we speak of a part as "anomalous" we mean that it varies at birth from the ordinary or typical form—it may be minute, as the small slip of a tendon, or large, as the addition of a complete vertebra to the spinal column. Wood has found that in the muscular system alone there are nine anomalies in the average individual. It is clear that the evolution of a new type, so far as the muscular system is concerned, must consist in the *accumulation of anomalies in a certain definite direction by heredity.* Thus the anomalous condition of one generation may become the typical condition of a very much later generation, and we observe the paradox of a typical structure becoming an anomaly and an anomalous structure becoming typical; for example, the supracondylar foramen of the humerus was once typical; it is now anomalous; the retardation in development of the wisdom tooth was once anomalous; it is now typical.

The same principle applies to races which are in different stages of evolution; an anomaly in the white, such as the early closure of the cranial sutures, is normal in the black. Now the deductions of the Weismann school of evolutionists seem to be founded upon the principle "*de minimis non curat lex;*" that we need only regard such major variations as can, *ex hypothesi*, weigh in the scale of survival. Against this I urge that we must regard the evolution of particular structures, the components of larger organs, the separate muscles and bones for example, for the very reason that while in some cases they play a most humble *rôle* in our economy we can prove beyond a doubt that they are in course of evolution. Minor variations in foot structure, which are possibly of vital importance to a quadruped whose very existence may depend upon speed, sink into obscurity as factors in the survival of the modern American.

The evolution of man in the most unimportant details of his structure promises, therefore, to afford a far more crucial test of the Lamarckian *vs.* the pure Natural Selection theory,

than in the domain of his higher faculties, for the reason that Selection may operate upon variations in mind, while it taxes our credulity to believe it can operate upon variations in muscle and bone. This is my ground for selecting the skeleton and muscles for the subject of the introductory lecture. Nevertheless, let us review variation in all its forms in human anatomy before forming an opinion. Let us remember, too, that congenital and acquired variations are universal as necessities of birth and life; they are exhibited in the body as a whole—in its proportions, in the components of each limb, finally in the separate parts of each component, as in the divisions of a complex muscle. Thus the possibilities of transformism are everywhere. What is the nature and origin of congenital variations? Their causes? Do they follow certain directions? Do they spring from acquired variations by heredity? These are some of the questions which are still unsettled.

But striking as are the anomalies from type, the repetitions of type as exhibited in atavism and normal inheritance are still more so, and equally difficult to explain. Therefore our theory must provide both for the observed laws of repetition of ancestral form and the laws of variation from ancestral form, as the pasture-land of evolution. Add to these, that for a period in each generation this entire legislation of nature is compressed into the tiny nucleus of the fertilized ovum, and the whole problem rises before us in the apparent impregnability which only intensifies our ardor of research.

The anthropologists and anatomists have enjoyed a certain monopoly of *Homo sapiens*, while the biologists have directed their energies mainly upon the lower creation. But under the inspiring influences of the Darwinian theory these originally distinct branches have converged, and as man takes his place in the zoological system, comparative anatomy is recognized as the infallible key to human anatomy.

For our present purpose we must suppress our sentiment at the outset and state plainly that the only interpretation of our bodily structure lies in the theory of our descent from some early member of the primates, such as may have given rise

also to the living Anthropoidea. This is also the only tenable teleological view, for many of our inherited organs are at present non-purposive, in some cases even harmful, as the appendix vermiformis.

From the typical mammalian stand-point man is a degenerate animal; his senses are inferior in acuteness; his upright position, while giving him a superior aspect, entails many disadvantages, as recently enumerated by Clevenger,[1] for the body is not fully adapted to it; his feet are not superior to those of many lower Eocene plantigrades; his teeth are mechanically far inferior to those of the domestic cat. In fact, if an unbiased comparative anatomist should reach this planet from Mars he could only pass favorable comment upon the perfection of the hand and the massive brain! Holding these trumps, man has been and now is discarding many useful structures. I refer especially to civilized man, who is more prodigal with his inheritance than the savage. By virtue of the hand and the brain he is, nevertheless, the best adapted and most cosmopolitan vertebrate. The man of Néanderthal or Spy, with retreating forehead and brain of small cubic capacity[2] was limited both in his ideas and his powers of travel, yet he was our superior in some points of osteological structure. But the period of Néanderthal was recent compared with that in which some of our rudimentary organs were serviceable, such as the vermiform appendix or the panniculus carnosus[3] muscle. These rudiments, in turn, are neogenetic when we consider the age of the two antique sense organs in the optic thalamus, the remnants of the median or pineal eye and the pituitary body, both of which were undoubtedly present, and probably useful, in the recently discovered Silurian fishes!

[1]Disadvantages of the Upright Position, article in AMERICAN NATURALIST, 1884, p. 1.

[2]The remarkable skulls and skeletons which have recently been discovered at Spy remove all doubts as to the normal *i. e.*, racial character of the famous Néanderthal skull, which were entertained by Quatrefages and others. See Fraipont and Lohest, Archives de Biologie, 1887, p. 697.

[3]This is an epidermal or twitching muscle in the quadrupeds.

I mention these vestiges of some of the first steps in creation to illustrate the extraordinary conservative power of heredity (which is even more forcibly seen in our embryological development), partly also to show how widely our organs differ in age. Galton has compared the human frame to a new building built up of fragments of old ones; extend this back into the ages and the comparison is complete.

Development, Balance, Degeneration.—It is probable that none of our organs are absolutely static and that the apparent halt in the development of some is merely relative, as where a fast train passes a slow one. The numerous cases of arrested evolution in nature are always connected with fixity of environment, an exceptional condition with man, and we have ample evidence that some organs are changing more rapidly than others.

Adaptation to our changing circumstances is mainly effected by the simultaneous development and degeneration of organs which lie side by side, as in the muscles of the foot or hand; in terms of physiology, we observe the hypertrophy of adaptive organs and atrophy of inadaptive or useless organs. This compensating readjustment, whereby the sum of nutrition to any region remains the same during redistribution to its parts, may be called metatrophism. It is the gerrymander principle in nature.

In practical investigation it is very difficult in many cases to determine whether an organ is actually developing or degenerating at the present time; although its variability or tendency to present individual anomalies indicates that some change is in progress. I may instance the highly variable peroneus tertius muscle (Wood). The rise or fall of organs is so constantly associated with their degree of utility that in each case the doubt can be removed by a careful analysis of the greater or less actual service rendered by the part in question. Apart from the question of causation it is a fixed principle that a part degenerating by disuse in each individual will also be found degenerating in the race.

Degeneration is an extremely slow process; both in the muscular and skeletal systems we find organs so far on the down grade that they are mere pensioners of the body, drawing pay (*i. e.*, nutrition) for past honorable services without performing any corresponding work—the plantaris and palmaris muscles for example. Of course an organ without a function is a disadvantage, so that the final duty of degeneration is to restore the balance between structure and function by placing it *hors de combat* entirely. One symptom of decline is variability, in which the organ seems to be demonstrating its own uselessness by occasional absence. As Humphrey remarks: "The muscles which are most frequently absent by anomalies are in fact those which can disappear with least inconvenience, either because they can be replaced by others or because they play an altogether secondary *rôle* in the organism." The stages downward are gradual; the rudiment becomes variable as an adult structure, then as a fœtal structure; the percentage of absence slowly increases until it reappears only as a reversion; finally the part ceases even to revert and all record of it is lost. This long struggle of the destructive power of degeneration, which you see is essentially an adaptive factor, against the protective power of heredity is the most striking feature of the law of Repetition. (See Galton's similar principle of Regression in Anthropology).

A careful study of our developing, degenerating, rudimental and reversional organs amply demonstrates that man is now in a state of evolution hardly less rapid, I believe, than that which has produced the modern horse from his small five-toed ancestor. As far as I can see the only reason why our evolution should be slower than that of the ancient horse is the frequent intermingling of races, which always tends to resolve types which have specialized into more generalized types. Wherever the human species has been isolated for a long period of time divergence of character is very marked, as will be seen in some of the races I refer to below.

To lighten the long catalogue of facts, gathered from many authors, I shall frequently allude to *habit*, but will ask you to consider it for the time as associational rather than casual.

Pouchet says: "Man is a creature of the writing-table and could only have been invented in a country in which covering of the feet is universal;" he should have added the "eating-table." From the average man our fashions and occupations demand the play of the forearm and hand, the independent and complex movements of the thumb and finger; the outward turning of the foot in walking. These are some of the most conspicuous features of modern habit.

The Skeletal Variations.[1]—In a most valuable essay by Arthur Thomson upon "The Influence of Posture on the Form of the Articular Surfaces of the Tibia and Astragalus in the Different Races of Man and the Higher Apes,"[2] we find clearly brought out the distinction between congenital variations and those which may be acquired by prolonged habits of life. It is perfectly clear from this investigation that certain racial characters, such as "platycnemism" or flattened tibia, which have been considered of great importance in anthropology, may prove to be merely individual modifications due to certain local and temporary customs. Thomson's conclusions are that the tibia is the most variable in length and form of any long bone in the body. Platycnemia is most frequent in tribes living by hunting and climbing in hilly countries, and is associated with the strong development of the tibialis posticus. The great convexity of the external condyloid surface of the tibia in savage races appears to be developed during life by the frequent or habitual knee flexure in squatting; it is less developed where the tibia has a backward curve and is independent of platycnemia. Another product of the squatting habit is a facet formed upon the neck of the astragalus by the tibia. This is very rare in Europeans; it is found in the gorilla and orang, but rarely in the chimpanzee. We must therefore be on our guard to distinguish between congenital or hereditary skeletal characters which are fundamental and "acquired" skeletal variations which may not be hereditary. The latter

[1]For recent general articles see Blanchard, L'Atavisme chez l'Homme, Rev. de Anthrop. 1885, p. 425; and Baker, The Ascent of Man, Proceedings of the American Association for the Advancement of Science, 1890.

[2]Journal of Anatomy and Physiology, 1889, p. 617.

are of questionable value in tracing lines of descent, if not actually misleading; on the other hand, the teeth, as shown by Cope in his essay on "Lemurine reversion in human dentition," have distinct racial patterns and are reliable indices of consanguinity because their form cannot be modified during life.

The main features of present evolution in the backbone are the elaboration of the spines of the cervical vertebræ, the increase of the spinal curvatures, the shortening of the centra of the lumbar vertebræ and shifting of the pelvis upward, whereby a lumbar vertebra is added to the sacrum and subtracted from the dorso-lumbar series.

Cunningham[1] has found that the division of the neural spines in the upper cervical vertebræ distinguishes the higher races from the lower. The spine of the axis is always bifid, but the spines of the cervicals three, four and five are also, as a rule, bifid in the European, while they are single in the lower races. The same author shows[2] that the bodies of the lumbar vertebræ are altering, by widening and shortening, to form a firmer pillar of support, with a compensating increase in the length of the intervertebral cartilages. In the child the vertebræ present more nearly their primitive elongate compressed form. With this is associated an increase of the forward lumbar curvature (Turner);[3] the primitive (*i. e.*, Simian) curve was backward; even in the negroes the collective measurement of the posterior faces of the five lumbars is greater than the anterior, in the proportion of 106 to 100; whereas in the white the collective anterior faces exceed the posterior in nearly the same proportion—100 to 96.

The lower region of the back is also the seat of one of the most interesting and important of the changes in the body, namely, the correlated evolution of the inferior ribs, the lumbar vertebræ and the pelvis—to which embryology, adult and comparative anatomy and reversion all contribute their quota of proof. In most of the anthropoid apes, and therefore pre-

[1] Ibid., 1886, p. 636.
[2] Journal of Anatomy and Physiology, 1890, p. 117.
[3] Ibid., 1887, p. 473.

sumably in the pro-anthropos, there are thirteen complete ribs and four lumbar vertebræ, while man has twelve ribs and five lumbars. Thus we may consider the superior lumbar of adult man as a ribless dorsal; not so in the human embryo, however, for Rosenberg[1] has found a cartilaginous rudiment of the missing 13th rib upon the so-called first lumbar. Atavism contributes an earlier chapter in the history of this region, for Birmingham[2] reports, out of fifty cases examined in one year, two in which there were six lumbars, and in each the 13th rib was well developed; this is an interesting example of "correlated reversion," for as the pelvis shifted downward to its ancestral position upon the 26th vertebra the 13th rib was also restored. The other ribs are in what the ancients styled a "state of flux;" our 8th rib has been so recently floated from the sternum that, and according to Cunningham,[3] it reverts as a true rib in twenty cases out of a hundred, showing a decided preference for the right side. Regarding also the occasional fusion of the 5th lumbar with the sacrum and the unstable condition of the 12th rib, which is, by variation rudimentary or absent, Rosenberg makes bold to predict that in the man of the future the pelvis will shift another step upward to the 24th vertebræ and we shall then lose our 12th rib. The upright position and consequent transfer of the weight of the abdominal viscera to the pelvis may be considered the habit associated with this reduction of the chest; at all events, in the evolution of quadrupeds there is a constant relation of increase between the size of the posterior ribs and the weight of the viscera, until the rib-bearing vertebræ rise to twenty and the lumbars are reduced to three.[4] It would be interesting to note the condition of the ribs in some of the large-bellied tribes of Africans in reference to this point.

The coccyx has naturally been the center of active search for the missing flexible caudals. As is well known, the adult coccyx contains but from three to five centers, while the embryo contains from five to six. Dr. Max Bartels has made "Die geschwänzten Menschen" the subject of an exhaustive

[1]Morph. Jahrb., 1876.
[2]Journal of Anatomy and Physiology, 1891, p. 526.
[3]Ibid., 1890, p. 127.
[4]In the elephant and rhinoceros.

memoir upon cases of the reversion of the tail, while Testut records all the primitive tail muscles in various stages of reversion. Watson reports that the curvatores coccygia (-depressores caudæ) only occur in 1 in 1000 cases.

This suggests a moment's digression to consider the different phases of reversion. The 13th rib recurs by what Gegenbaur[1] calls "neogenetic reversion," for it is simply the anomalous adult development of an embryonic rudiment. Under neogenetic reversions many authors also include cases of the "arrested development," or persistence of an embryonic condition to adult life, such as the disunited odontoid process of the axis vertebra, which happens to repeat a very remote ancestral condition. I think such cases may illustrate a reversional tendency, although many cases of arrested development, such as anencephaly, have no atavistic significance whatever.[2] More rare and far more difficult to explain are the "palæogenetic reversions," in which the anomaly, such as the supracondylar foramen, reverts to an atavus so remote that the rudiment is not even represented in the embryo.

The features of skull development are primarily the increase of the cranium and the late closure of the cranial sutures in contrast with the more complete and earlier closure of the facial sutures.

So far as I can gather this seems to be another region where the white and colored races present reversed conditions; the early closure and arrest of brain development in the negroes is well known; the later closure among the whites is undoubtedly an adaptation to brain growth. In his valuable statistics upon the Cambridge students Galton says: "Although it is pretty well ascertained that in the masses of population the brain ceases to grow after the age of nineteen, or even earlier, it is by no means the case with university students. In high honor men headgrowth is precocious, their heads predominate over the average more at nineteen than at twenty-five."

Many of the cases of arrested closure of facial sutures are reversional, as they correspond with the adult condition of

[1]Morph. Jahrb., Bd. vi, p. 585.

[2]Anencephaly, it should be said, is frequently associated with numerous reversions.

other races, such as the divided malar or os Japonicum. The human premaxillary, a discovery with which Goethe's name will always be associated, is sometimes partially, more rarely wholly, isolated; it is late to unite with the maxillary in the Australians, and has been reported entirely separate in a New Caledonian child (Deslongchamps) and in two Greenlanders (Carus). The orbito-maxillary frontal suture, cited by Turner as a reversion to the pithecoid condition, is believed by Thomson,[1] after the examination of one thousand and thirty-seven skulls, to be merely an accidental variation, without any deeper significance. The development of the temporal bone from two centers, observed by Meckel, Gruber and many others, is considered by Albrecht a reversion to the separate quadrate of the sauro-mammalia. This I think is in the highest degree improbable (see "Limits of Reversion"). The open cranial and closed facial sutures are apparently associated with our increasing brain action and decreasing jaw action; in one case the growth is prolonged and the sutures are left open, in the other the growth is arrested and the sutures are closed.

Is the lower jaw developing or degenerating? This question has recently been the subject of a spirited controversy between Mr. W. Platt Ball,[2] representing the Weismann school, and Mr. F. Howard Collins,[3] supporting Herbert Spencer's view that a diminishing jaw is one of the features of our evolution which can only be explained by disuse. Mr. Collins finds that, relatively to the skull, the mass of the recent English jaw is one-ninth less than that of the ancient British, and roughly speaking, half that of the Australian. He appears to establish the view that the jaw is diminishing.

Closely connected with this is the evolution of the teeth; how are they tending? This we will consider below.

Variations of the Teeth.—Flower[4] has shown, as regards the length of our molar series, that we, together with the ancient

[1]Journal of Anatomy and Physiology, 1890, p. 348.

[2]Are the Effects of Use and Disuse Inherited? Nature Series, 1890.

[3]The Lower Jaw in Civilized Races, 1891.

[4]Journal of the Anthropological Institute, 1880.

British and Egyptians, belong to a small-toothed or "microdont" race; the Chinese, Indians (North American), Malayans and Negroes in part are intermediate or "mesodont," while the Andamanese, Melanasions, Australians and Tasmanians are "macrodont." While undersize marks the molars as a whole the wisdom tooth is certainly in process of elimination; it has the symptoms of decline; it is very variable in size, form and in the date of its appearance; is often misplaced, and is not uncommonly quite rudimentary (Tomes).[1] Here is another instance where the knife-and-forkless races reverse our degeneracy, for in them not only is the last normal molar (m. 3) large and cut long before the traditional years of discretion, but in the first two lower molars are found two intermediate cusps (Tomes)[2] which are variable or absent in us (Abbott); moreover, in the macrodont races a surplus molar[3] (m. 4) is sometimes developed. Mummery reports nine such cases among three hundred and twenty-eight West Africans (Ashantis). As an instance of associated habit I may here mention that Dr. Lumholtz, the Australian explorer, informs me that in adult natives the teeth are worn to the gum; in the absence of tools they are used in every occupation, from eviscerating a snake to cutting a root. A tour of inspection through any large collection of skulls brings out the contrast between the sound and hard-worn molars of the savage and the decayed and little-worn molars of the white.

Upon the descent theory the reduction of teeth in the progenitor of man began as far back as the Eocene period, for not later than that remote age do we find the full complement of three incisors and four premolars in each jaw; now there are but two remaining of each. Baume, a high authority, believes he has discovered eleven cases of a rudimental reversion of one of these lost premolars[4] not cutting the jaw. Not infrequently both these missing teeth occur by reversion! It is

[1]Dental Anatomy, p. 416.

[2]Op. cit., p. 416.

[3]This tooth has been found in several other macrodont tribes (Australians, Tasmanians, Neo-Caledonians), Fontan.

[4]Odontologische Forschungen, p. 268. This rudiment is found between the first and second normal premolars.

difficult to conceive of reversion to such a remote period, yet it is supported by other evidence. An embryonic third incisor has, I believe, been discovered. As long ago as 1863 Sedgwick[1] recorded a case of six upper and lower incisors in both jaws, and appearing in both the milk and permanent dentitions; this anomaly was inherited from a grandparent, a striking instance of hereditary reversional tendency. We might consider that these cases of supernumerary teeth belonged in the same category as polydactylism or additional fingers, which are not atavistic, but for the fact that they do not exceed the typical ancestral number, whereas the fingers do.

We owe to Windle[1] a careful review of the incisor reversions in which he shows that the lost incisors reappear more frequently in the upper than the lower jaw (coinciding with the fact that the lower teeth were the first to disappear in the race); he considers that the lost tooth was the one originally next the canine, and concludes by adding our present upper outer incisor to the long list of degenerating organs.[3] He supports this statement by measurements and by citing cases in which it has been found absent. Yet the reduction of the jaws is apparently outstripping that of the teeth, if we can judge from the frequent practice among American dentists of relieving the crowded jaw by extraction.

We now turn to the arches and limbs. Flower has pointed out that the base of the scapula is widening in the higher races, so that the "index," or ratio of length to breadth is quite distinctive. Gegenbaur associates this with the development of the scapulo-humeral muscles and the greater play of the humerus as a prehensile organ.

In general, the arm increases in interest as we descend toward the hand, both in the skeleton and musculature, because here we meet with the first glimpses of facts which enable us to form some estimate of the rate of human evolution. The well-known humeral torsion (connected with

[1]British and Foreign Medico-Chirurgical Review, 1863.

[2]Journal of Anatomy and Physiology, 1887, p. 85.

[3]Baume believes that the missing incisor is the primitive median one, while Turner believes it is the second. The fossil record supports Windle.

increased rotation) ascends from 152° in the polished stone age to 164° in the modern European. The intercondylar foramen or perforation of the olecranon fossa is exceptionally well recorded;[1] it is found in thirty per cent. of skeletons of the reindeer period; in the dolmen period it fell to twenty-four per cent.; in Parisian cemeteries[3] between the fourth and tenth centuries it is found in 5.5 per cent.; it has now fallen to 3.5 per cent. The condylar foramen, occasionally forming a complete bridge of bone above the inner condyle and transmitting the median nerve and brachial artery, is known as the "entepicondylar" foramen in comparative anatomy, and is one of the most ancient characters of the mammalia; it reverts palæogenetically in one per cent. of recent skeletons, but much more frequently in inferior races (Lamb). In the wrist-bone is sometimes developed another extremely old structure—the os centrale. Gruber[2] reported its recurrence at .25 per cent. approximately. This is a case of neogenetic reversion, for Leboucq[3] shows that there is a distinct centrale in every human carpus in the first part of the second month, which normally fuses with the scaphoid by the middle of the third month.

The divergence of the female from the male pelvis is an important feature of our progressive development; it is proved by the fact that as we descend among the lower races it becomes increasingly difficult to distinguish the female skeleton from the male, for the pelves of the two sexes are nearly uniform. Here it seems to me is a most interesting problem for investigation. Arbuthnot Lane's[3] views of the mechanical causes of this divergence, which are strongly Lamarckian, may be weighed with the theory of survival of the fittest, for a large female pelvis is perhaps the best example that can be adduced of a skeletal variation which would be preserved by natural selection for reasons which are self-evident. The third trochanter of the femur is believed by Professor Dwight,[4] of

[1]See Blanchard, op. cit., p. 450.

[2]Virchow's Archiv, 1885, p. 353.

[3]Ann. de la Soc. de Med. de Gand, 1884.

[3]Journal of Anatomy and Physiology, 1888, p. 214.

[4]Ibid., 1890, p. 61.

the Harvard Medical School, to be a true reversion (one per cent.) in our race and not an acquired variation, as it is very frequently found among the Sioux (fifty per cent.), Laplanders sixty-four per cent., and Swedes thirty-seven per cent.; like the condylar foramen it is an ancient mammalian character.

The foot is full of interest in its association of degeneration and development with our present habits of walking; the great toe is increasing and the little toe diminishing, causing the oblique slope from within outward which is in wide contrast with the square toes in the infant or in the lower races. In many races the second toe is as long as the first, and the feet are carried parallel instead of the large toe turning out. If anyone will analyze his sensations in walking, even in his shoes, he will be conscious that the great toe is taking active part in progression, while the little toe is passive and insensitive. We are not surprised, therefore, to learn from Pfitzner[1] that we are losing a phalanx, that in many human skeletons (41.5 per cent. in women and thirty-one per cent. in men) the two end joints of the little toe are fused. The fusion occurs not only in adults but between birth and the seventh year, and in embryos of between the fifth and seventh month. The author does not attribute this to the mechanical pressure of tight shoes because it is found in the poorer classes. He considers it the first act of a total degeneration of the fifth toe.

Variations in the Muscles.—The evolution of the muscles of the foot looks in the same direction.

As you know, the large toe in many of the apes is set at an angle to the foot and is used in climbing. It is still employed in a variety of occupations by different races. According to Tremlett[2] the celebrated great toe of the Annamese, which normally projects at a wide angle from the foot, is contemptuously mentioned in Chinese annals of 2285 B.C., the race being then described as the "cross-toes." The long flexor of the hallux is apparently degenerating, showing a tendency to

[1]See Humboldt, 1890; also Nature, 1890, p. 301.

[2]Journal of the Anthropological Institute, 1880, p. 461.

fuse with the flexor communis: the abductors and adductors of this toe are also degenerating, the latter being proportionately large in children (Ruge). The little toe exhibits only by reversion its primitive share of the flexor brevis (Gegenbaur); more frequently it varies in the direction of its future decline by losing its flexor brevis tendon entirely. Two atavistic muscles, the abductor metatarsi quinti[1] (always present in the apes), and the peroneus parvus (Bischoff), also point to the former mobility of the outer side of the foot. In general the bones of the foot are developing on the inner and degenerating on the outer side, with loss of the lateral movements of the hallux and of all independent movements in the little toe. The associated habit is that the main axis of pressure and strain now connects the heel and great toe, leaving the outer side of the foot comparatively functionless.

The variations in the muscular system mark off more clearly the regions of contemporary evolution, and therefore are even more instructive than those in the skeleton. Muscular anomalies have, however, never been adequately analyzed. Even the remarkable memoir of M. Testut, "Sur les anomalies musculaires," is defective in not clearly distinguishing between variations which look to the future, those which revert to the past, and those which are fortuitous, for the author is strongly inclined to refer all anomalies to reversion.

The law of muscular evolution is specialization by the successive separation of new independent contractile bands from the large fundamental muscles, while the law of skeletal evolution is reduction of primitive parts and the specialization of articular surfaces. The number of muscles in the primates as a whole has, therefore, been steadily increasing, while the number of bones has been diminishing. In man the number of muscles is probably increasing in the regions of the lower arm and diminishing in every other region. The analysis is rendered very difficult by the fact that some muscles (*e. g.*, those connecting the shoulder with the neck and back) revert to a former condition of greater specialization when they were employed in swinging the body by the arms, and in quadru-

[1]Darwin: Descent of Man, p. 42.

pedal locomotion; while other muscles (*e.g.*, those connecting the forearm and fingers) revert to a former simpler arrangement when the hand was mainly a grasping organ, and the thumb was not opposable.

As in the skeleton, we find that muscular anomalies include, 1, palæogenetic reversions, or complete restorations of lost muscles; 2, neogenetic reversions, or revivals of former types in the relations of existing muscles; 3, progressive variations, which either by degeneration or specialization point to future types; 4, fortuitous variations, which cannot be referred to either of the above.

Duval observes that the flexor longus pollicis repeats in reversion all the stages of its evolution between man and the apes, in which it is a division of the flexor profundus. Gruber and others have even observed the absence of the thumb tendon. This is true of all the new muscles. Of this Testut writes: "Ne dirait-on pas, en le voyant s'éloigner si souvent de son état normal, que la nature voudrait le ramener à sa disposition primitive, luttant ainsi sans cesse contre l'adaptation, et ne lui abandonnant qu' à regret l'une de ses plus belles conquêtes."

Speaking of the hand, Baker[1] says: "On comparing the human hand with that of the anthropoids, it may be seen that this efficiency is produced in two ways—first, increasing the mobility and variety of action of the thumb and fingers; second, reducing the muscles used mainly to assist prolonged grasp, they being no longer necessary to an organ for delicate work requiring constant readjustment." You have noticed the recent discovery that the grasping power of infants is so great that the reflex contraction of the fingers upon a slender cross bar sustains their weight; this power and the decided inward rotation of the sole of the foot and mobility of the toes are persistent adaptations. Our grasping muscle, the palmaris longus, is highly variable and often absent; like the plantaris of the calf, it has been replaced by other muscles, and its insertion has been withdrawn from the metapodium to the palmar fascia. In negroes we frequently find the palmaris

[1]Op. cit., p. 299.

reverting to its former function of flexing the fingers by insertion in the metacarpals.

The rise of muscular specialization by degeneration is beautifully shown in the extensor indicis, which, while normally supplying the index only, reverts by sending its former slips to the thumb, middle, and even to the ring finger. Testut[1] believes that the extension power of the middle and ring fingers has declined, as the cases of reversion point to greater mobility; the extensor minimi digiti is distinct and highly variable (Wood), often sending a slip to the ring finger.

The entire flexor group of the hand, excepting the palmaris, is apparently specializing. The demonstration by Windle[2] and Bland Sutton, that the origin of the flexors and entensors is shifting downward from their original position, is evidence of an adaptation to the short special contractions required of them.

The abductor pollicis[3] is also progressive and variable (Wood); the reduplication of its inferior tendon, which is sometimes provided with a distinct muscle, apparently points to the birth of a second abductor. The opponens of the thumb is well established and constant. Variability seems to characterize both the developing and degenerating muscles; the latter are apt to be absent; it is rare that an important muscle, such as the extensor indicis, is absent, but such cases are reported.

It is interesting to note that the lost muscles of the body are almost exclusively in the trunk or shoulder, and pelvic arches, and not in the limbs. It will be remembered that the human shoulder-joint is exceptionally rigid, whereas in the quadrupedal state it was a factor in progression. Some of the muscular reversions in this quadrupedal region are the levator claviculæ (1 to 60, Macalister), trachelo-clavicularis, scalenus intermedius, acromio-basilaris (Champneys), transversus nuchæ (Gegenbaur). Apparently associated with the former swinging of the body by the fore-limb in the arboreal life are the

[1]Op. cit., p. 564.

[2]Journal of Anatomy and Physiology, 1890, p. 72.

[3]Or extensor ossis metacarpi pollicis. See Testut, p. 553.

atavistic coraco-brachialis-brevis (Testut), the epitrochleo-dorsalis (Testut), and pectoralis tertius (Testut).[1]

Centers of Variability.—As the literature is so readily accessible I will not multiply illustrations of the innumerable congenital variations related to human evolution. I call attention to several important inductions. First, there are several centers in which both the skeletal and muscular systems are highly variable. Second, that the most conspicuous variations, and therefore the most frequently recorded, are reversions. Third, that structure lags far behind function in evolution.

The conclusions of Wood and Testut[2] are that variability is independent of age or sex, of general muscularity, and of abnormal mental development. Wood found 981 anomalies in 102 subjects; of these, 623 were developed upon both sides of the body, while 358 were unilateral. Of still greater interest are the statistics collected by Wood between 1867–68 in the dissecting-room of King's College, upon 36 subjects (18 of each sex). These show that there are more anomalies in the limbs than in the trunk; that anomalies are rare in the pelvis; that there were 292 anomalies in the anterior limbs to 119 in the posterior; that in both limbs the anomalies increase toward the distal segments, culminating in the muscles of the thumb, where they rise to ninety per cent. (mainly flex. long. pollicis, and abd. long. pollicis). These facts seem to prove conclusively that while variation is universal it rises to a maximum in the centers where human evolution is most rapid; here are Herbert Spencer's conditions of unstable equilibrium. This has a direct bearing, as I shall show, upon our theory of heredity.

Fortuitous Congenital Variations.—I have thus far considered only those variations which apparently have a definite relation to the course of human evolution. There is an

[1]Quain describes seventy anomalous muscles (Anat., Vol. I.) Testut describes a still larger number.

[2]Op. cit., p. 760.

entirely different class of congenital variations which may be described as fortuitous or indefinite because they do not occur in any fixed percentage of cases; they are liable to take any direction; they cannot be considered reversional because they are not found in the hypothetical atavus, and there is not sufficient evidence to cause us to consider them as incipient features of our future structure.

Some may not be truly congenital (*i.e.*, springing direct from the germ-cells) but may be merely deviations from the normal course of development. I may instance the variations in the carpus recorded by Turner[1] in which the trapezium and scaphoid unite, or the trapezoid and semi-lunar divide, or the astragalus and navicular unite (Anderson).

The best examples of fortuitous congenital variations are seen in supernumerary fingers and vertebræ. The eighth cervical vertebra, bearing a rudimentary rib,[2] is not a reversion because the most remote ancestors of man have but seven cervicals. In cases where a rib is developed upon the seventh cervical, however, the reversion theory is perhaps applicable because rib bearing cervicals are relatively less remote. The same distinction applies to polydactylism. How absurd it is to consider a sixth finger atavistic, when we remember that even our Permain ancestors had but five fingers.

We cannot, however, class as purely fortuitous a variation which occurs in a definite percentage of cases presenting twenty-four different varieties, but occurring in the same region. Such is the much-discussed[3] musculus sternalis, a muscle extending vertically over the origin of the pectoralis from the region of the sterno-mastoid to that of the obliquus externus. Testut lightly applies his universal reversion theory, and as this muscle is not found in any mammal considers it a regression to the reptilian presternal (Ophidia)! Turner also considered it as reversional in connection with the panniculus carnosus, the old twitching muscle of the skin, which plays so many freaks of reversion in the scalp and neck; this

[1]Journal of Anatomy and Physiology, 1884, p. 245.

[2]Arb. Lane: Journal of Anatomy and Physiology, 1885, p. 266.

[3]See Turner, Shepherd, and Cunningham: Journal of Anatomy and Physiology.

view is negatived by the fact that this muscle is innervated by the anterior thoracic (Cunningham, Shepherd) which would connect it with the pectoral system, or by the intercostal nerves (Bardeleben). Although the high percentage of recurrence in the sternalis in anencephalous monsters (ninety per cent. according to Shepherd) supports the reversion view, it is offset by the high percentage (four per cent.) in normal subjects, for this is far too high for a structure of such age as the reptilian presternal. Cunningham has advanced another hypothesis, first suggested by the frequency of this anomaly in women, that this is a new inspiratory muscle, having its origin in reversion, but serving a useful purpose when it recurs, and therefore likely to be perpetuated.

These fortuitous variations, as well as variations in the proportions of organs, play an important part in the present discussion upon heredity, for it is believed by the Weismann school that such variations, if they chance to be useful, will be accumulated by selection and thus become race characters.

The Limits of Reversion.—There is such a wide difference of opinion upon the subject of reversions that it is important to determine what are some of the tests of genuine reversions? How shall we distinguish them from indefinite variations or from anomalies like the sternalis muscle, which strain the reversion theory to the breaking-point?

Testut,[1] Duval, and Blanchard take the extreme position that almost all anomalies reproduce earlier normal structures, and that the exceptions may be attributed to the incompleteness of our knowledge of comparative anatomy. I may here observe that popular as the descent theory has recently become in France, neither these anthropologists nor the palæontologists show a very clear conception of the phyletic or branching elements in evolution. If they do not find a muscle in the primates they look for it in other orders of mammals. Now, since these other branches diverged from that which gave rise to man at a most remote period, the dis-

[1] Op. cit., p. 4.

covery of a similar muscle may be merely a coincidence; it is by no means a proof of reversion.

The first test of reversion is therefore the anatomy of the atavus, and this is derived partly from the palæontological record of the primates, partly from the law of divergence, viz., that features which are common to all the living primates were probably also found in the stem form which gave rise to man; finally, from the comparative anatomy of the living anthropoidea.

The second test is whether a structure passes the limits of reversion as determined by cases of atavism in which there can be no reasonable doubt. Two of these phenomena have recently been discussed, which seem to extend the possibilities of reversion back to structures which were lost at a very remote period. I refer to papers by Williams and Howes. Williams[1] has analyzed 166 recorded cases of polymastism; he finds that supernumerary nipples of some form occur in two per cent., and that in all except four of the cases examined the anomalies, tested by position, etc., support the reversion hypothesis. In the living lemurs, which form a persistent primitive group of monkeys, we find that the transition from polymastism to bimastism is now in progress by the degeneration of the abdominal and inguinal nipples, it is fair to assume that the higher monkeys also lost their abdominal nipples at a primitive stage of development, and therefore that cases of multiple nipples indicate reversion to a lower Eocene condition! Howes[2] has recently completed a most interesting study of the "intranarial epiglottis," or cases in which the epiglottis is carried up into the posterior nares, as in young marsupials and some cetacea, to subserve direct narial respiration. This has now been observed to occur by reversion in all orders of mammals, including the monkeys and lemurs. One case has also been reported by Sutton of its occurrence in a human fœtus. This is apparently a human reversion to a structure much older than the age of the lemurs.

The third test is the inverse ratio to time. It would seem, *a priori*, that the percentage of recurrence of atavistic structures

[1]Journal of Anatomy and Physiology, 1891, p. 224.

[2]Ibid, 1889, p. 587.

should decrease as the extent of time elapsing since the structure disappeared increases. This law is apparently established in the case of the condylar and intercondylar foramina, and if we examine all the percentages which have been established, we see at once that they bear a ratio to time; compare the relative frequency of the ischio-pubic (fifty per cent.), dorso-epitrochlearis (five per cent.), and levator-claviculæ (1.66 per cent.) muscles with the periods which have elapsed since their past service. This is why it is so important to establish percentages for all our atavistic organs; fuller statistics will not only bear upon heredity, but I can conceive of their application to the extremely difficult problem of estimating geological time. We must, of course, establish as a standard cases of congenital variation in which the frequency of recurrence has been steadily declining in the same race between two known periods of time—an available structure is the intercondylar foramen or supratrochlear foramen, as recorded by Blanchard, Shepherd and others.

The reversional tendency is hereditary. There are many cases, both of reversions (as in the teeth) and indefinite variations being hereditary, that is, reappearing in several generations, or skipping a generation and recurring in the second.

Summary.—There are clearly marked out several regions in the human body in which evolution is relatively most rapid, such as the lower portion of the chest, the upper cervicals, the shoulder girdle in its relation to the trunk, the lower portion of the arm and hand, the outer portion of the foot. We notice that these regions especially are centers of adaptation to new habits of life in which new organs and new relations of parts are being acquired and old organs abandoned.

We observe, also, that all parts of the body are not equally variable, but these centers of evolution are also the chief centers of variability. The variations here are not exclusively, but mainly, of one kind; they rise from the constant struggle between adaptation and the force of heredity. Here is a muscle like the extensor indicis attempting to give up an old function and establish a new one; it maintains its new func-

tion for several generations and then goes back without any warning to a function which it had thousands of years ago. Thus the force of reversion strikes us as a universal factor.

Now the singular fact about reversion is the frequent proof it affords of what Galton has called " particulate inheritance." When the extensor indicis reverts all the muscles around it may be normal; therefore we are obliged to consider each of these muscles as a structure by itself, with its own particular history and its own tendencies to develop or degenerate. Thus it is misleading to base our theory of evolution and heredity solely upon entire organs; in the hand and foot we have numerous cases of muscles in close contiguity, one steadily developing, the other steadily degenerating. Reversion very rarely acts upon many structures at once; when it does we have a case of diffused anomaly, some repetition in the epidermis or in the entire organism of a lower type. Yet in spite of reversion and the strong force of repetition in inheritance, the human race is steadily evolving into a new type. We must, it seems to me, admit that an active principle is constantly operating upon these particular structures, guiding them into new lines of adaptation, acting upon widely separate minor parts or causing two parts, side by side, to evolve in opposite directions, one toward degeneration the other toward development.

I may now recall the two opposed theories as to what this active principle is:

The first, and oldest, is that individual adaptation, or the tendencies established by use and disuse upon particular structures in the parent are, in some degree, transmitted to the offspring, and thus guide the main course of variation and adaptation.

The second is that all parts of the body are variable, and that wherever variations take a direction favorable (that is adaptive) to the survival of the parent they tend to be preserved; where they take the opposite direction they tend to be eliminated. Thus, in the long run, adaptive variations are accumulated and a new type is evolved.

Partial Table of Characters in Evolution.

Principal Regions of Evolution.	Developing Organs.	Degenerating Organs.				
		Retrogressive.	Variable.	Rudimentary (occasionally absent)	Reversional (from embryo).	Reversional (from germ-cells).
Skull and jaw.	Cranium.	Facial sutures.			Premaxillary.	
Spinal curvatures.		Infer. maxilla.				
		Hyoids.	Lumbars and pelvis.	Coracoid.		
Cervicals, lumbars, and coccyx.	Female pelvis.		Coccygeal vert.	4th and 5th caudals.	5th and 6th caudals.	Caudals +
Lower ribs.		8th rib.	12th rib.		13th rib.	7th cerv. ribs.
Scapula and lower humerus.	Scapula.					Condylar for.
	Clavicle.					S. trochlear. for.
Outer side of pes.	Hallux.	4th and 5th digits of pes.	Terminal phalanx of 5th dig. of pes.			3d trochanter.
	Tibia.				Centrale-manus.	
					Intermedium, pes.	
Teeth..........	....	Canines..........	....	....	? Lateral incisor.	.......×.......
		Incisors, lateral sup. 3d molar.			? Third premolar.	4th premolar.
			3d molar.			
Flexors and extensors of arms..........	Flex. prof. and perf.	....	....	Paniculus carnosus.	.......×.......	Trans. nuchæ.[1]
	Extensor indicis.	Muscles of mastica'n				Epitrochl. dors.
	Flex. long. pollicis.					Acromio-basilar.
	Abd. long. pollicis.					Levator-claviculæ.
	Flex. long. hallucis.					Pect. tertius.
						Cor. brach. brev.
		Pyramidalis.				Ischio-pubic.
Shoulder to trunk.	Triceps extensor surae.	Psoas parvus.				Depressores caudæ.
Trunk to femur.						Scansorius.
	Glutæal group.	Abd. and add. hallucis.	Muscles, 5th toe.	Plantaris.		Abd. metars. 5th.
	Facial group.			Palmaris.		Peroneus parvus.

[1] It is probable that some of these muscles are represented in the fœtus.

It is evident at once, from a glance over the facts brought forward in this lecture, that the first theory is the simplest explanation of these facts; that use and disuse characterizes all the centers of evolution; that changes of structure are slowly following our changes of function or habit.

But while the first explanation is the simplest it by no means follows that it is the true one. In fact, it lands us in many difficulties, so that I shall reserve the *pros* and *cons* for my second lecture upon Heredity. The Lamarckian theory is a suspiciously simple explanation of such complex processes.

(*To be continued.*)

NOTE.—Since this lecture was written I have received copies of Topinard's "L' Homme dans la Nature," Paris, 1891, and of Wiedersheim's "Der Bau des Menschen als Zeugniss für seine Vergangenheit." The latter is full but not critical.